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ECOLOGICAL CRITERIA FOR EVALUATING CANDIDATE SITES FOR MARINE RESERVES

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Abstract. Several schemes have been developed to help select the locations of marine reserves. All of them combine social, economic, and biological criteria, and few offer any guidance as to how to prioritize among the criteria identified. This can imply that the relative weights given to different criteria are unimportant. Where two sites are of equal value ecologically, then socioeconomic criteria should dominate the choice of which should be protected. However, in many cases, socioeconomic criteria are given equal or greater weight than ecological considerations in the choice of sites. This can lead to selection of reserves with little biological value that fail to meet many of the desired objectives. To avoid such a possibility, we develop a series of criteria that allow preliminary evaluation of candidate sites according to their relative biological values in advance of the application of socioeconomic criteria. We include criteria that, while not strictly biological, have a strong influence on the species present or ecological processes. Our scheme enables sites to be assessed according to their biodiversity, the processes which underpin that diversity, and the processes that support fisheries and provide a spectrum of other services important to people. Criteria that capture biodiversity values include biogeographic representation, habitat representation and heterogeneity, and presence of species or populations of special interest (e.g., threatened species). Criteria that capture sustainability of biodiversity and fishery values include the size of reserves necessary to protect viable habitats, presence of exploitable species, vulnerable life stages, connectivity among reserves, links among ecosystems, and provision of ecosystem services to people. Criteria measuring human and natural threats enable candidate sites to be eliminated from consideration if risks are too great, but also help prioritize among sites where threats can be mitigated by protection. While our criteria can be applied to the design of reserve networks, they also enable choice of single reserves to be made in the context of the attributes of existing protected areas. The overall goal of our scheme is to promote the development of reserve networks that will maintain biodiversity and ecosystem functioning at large scales. The values of ecosystem goods and services for people ultimately depend on meeting this objective.

Key words: biodiversity conservation; ecosystem functioning; ecosystem services; fisheries management; marine reserve selection; reserve evaluation criteria; reserve networks.

INTRODUCTION

For most of the 20th century, terrestrial ecosystems have received a much greater conservation priority than marine systems. However, increased access to the marine environment for scientists and public has led to

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TABLE 1. Social and economic criteria used to select the locations of marine protected areas.

Value	Criteria
Economic	Number of fishers dependent on the area
	Value for tourism
	Potential contribution of protection to enhancing or maintaining economic value
Social	Ease of access
	Maintenance of traditional fishing methods
	Presence of cultural artifacts/wrecks
	Heritage value
	Recreational value
	Educational value
	Aesthetic appeal
Scientific	Amount of previous scientific work undertaken
	Regularity of survey or monitoring work done
	Presence of current research projects
	Educational value
Feasibility/practicality	Social/political acceptability
	Accessibility for education/tourism
	Compatibility with existing uses
	Ease of management
	Enforceability

Note: Information summarized from Swedish Environmental Protection Administration (Naturvårdsverket 1995), Kelleher and Kenchington (1992), Nordic Council of Ministers (Nordiska Ministerrådet 1995), Salm and Price (1995), Hockey and Branch (1997), Agardy (1997), and Nilsson (1998).

an appreciation that conservation is needed as urgently in the sea as on land. We now use between a quarter and a third of the total primary production of the most productive marine ecosystems in the world (Pauly and Christensen 1995). This is similar to the proportion of terrestrial production we appropriate (Vitousek et al. 1997). In capturing this production we have been systematically depleting the highest trophic levels from marine food webs (Pauly et al. 1998), threatening some of the most valuable and spectacular of the marine megafauna, and disrupting the composition and functioning of marine communities and ecosystems, from kelp forests (Dayton et al. 1998) to coral reefs (Roberts 1995).

The seabed itself has been transformed by heavy fishing gear dragged across the bottom (Watling and Norse 1998). The scale and severity of these impacts has led to a sense of urgency that marine ecosystems must be protected quickly to avert an extinction crisis in the sea comparable to that occurring on land (Roberts and Hawkins 1999). At the same time, there has been a growing recognition that fully protected marine reserves, areas closed to all fishing and other disruptive or harmful human activities, will not only protect species and habitats but could significantly improve fishery management (Dugan and Davis 1993, Bohnsack 1996, Roberts 1997, Allison et al. 1998). This combination of conservation and management benefits has been a potent force in pushing ahead the establishment of marine reserves worldwide (National Research Council 2000). Many countries have now initiated ambitious programs to set up protected areas in the sea. However, if networks of marine reserves are to be introduced, managers need guidance on their placement which is firmly grounded in knowledge of how marine ecosystems work. In this paper, we develop a series of criteria that allow objective assessment of the biological value of candidate reserves.

Previous evaluation schemes

The evaluation scheme we outline below is not the first to have been devised for reserve selection. Nilsson (1998) has summarized four different schemes developed by Kelleher and Kenchington (1992), Salm and Price (1995), the Nordic Council of Ministers (Nordiska Ministerrådet 1995) and the Swedish Environmental Protection Agency (Naturvårdsverket 1980). Other schemes have been developed by Agardy (1997), Hockey and Branch (1997), and Day and Roff (2000). All of them combine biological with social and aesthetic criteria, including ecological, economic, social and scientific values, naturalness, national or international importance, and feasibility. Another set of criteria that has become increasingly relevant to the siting of marine reserves relates to their value to fisheries. Most authors subsume this under the economic value category but Hockey and Branch (1997) specifically separated fishery management from ecological and other social criteria when they developed a system for selection and evaluation of reserves in South Africa.

We limit consideration to biological criteria, or those underpinned by a knowledge of biology. Purely social criteria, such as accessibility for recreation and aesthetics, fall outside the domain of this paper. Table 1 lists the many factors in addition to biological criteria that must be taken into account when selecting reserve locations. Kelleher and Kenchington (1992) have said that where a choice exists between areas that are all

ecologically suitable, the final selection should be determined by socioeconomic criteria, and our philosophy has been to develop a process which generates such choices. Reserves whose objectives include conservation or fishery functions must have a solid foundation in biology to succeed. A reserve with little biological value will provide few benefits, just as a bank account with little money will yield almost no interest. Thus biological evaluation should generally precede and inform social and economic evaluation of potential reserve sites. We anticipate that this scheme will feed into a larger decision-making framework for marine-reserve networks, where economics and other social factors also play a part. Airamé et al. (2003) provide examples of how stakeholders with social and economic concerns can provide input in ways that do not compromise the biological integrity of reserves. It is important to stress here that although we propose biological evaluation comes before socioeconomic assessment, stakeholders must be involved from the very beginning. Their input is essential to the success of reserve design and establishment (Kelleher and Recchia 1998).

To achieve conservation objectives, reserves that are valuable for their biodiversity need to be chosen. But they, or the management schemes in which they are embedded, must also incorporate the ecological processes which support that diversity. To achieve fishery objectives, it is necessary that reserves will be productive within their boundaries (i.e., either self sustaining or receiving propagules from elsewhere) but will also allow the transfer of that production to fishing areas. For these reasons, the selection criteria we develop concentrate on the evaluation of sites according to their biodiversity, the processes that will lead to the long-term sustainability of that diversity, and processes that will aid fisheries management and provide a plethora of other human benefits. Criteria that capture biodiversity values of sites include biogeographic representation, habitat heterogeneity, and endemism. Criteria that capture sustainability of biodiversity and fishery values include the presence of exploitable species, vulnerable life stages, connectivity between reserves, links among habitats, the provision of ecosystem ''services'' for humans, and other criteria that assess the magnitude of human and natural threats to the viability of candidate areas.

Selection Criteria

Biogeographic representation

Coverage of all biogeographic regions is a prerequisite for protection of biodiversity. Hockey and Branch (1994), Ballantine (1997), Day and Roff (2000), and others have argued that representing all the different biogeographic regions in a protected-area network should be a core conservation objective, because assemblages of species will be distinct in each.

Two of the criteria developed in other schemes, the presence of representative species or habitats and the presence of species at their range boundaries (Hockey and Branch 1997, Nilsson 1998), relate directly to, and are incorporated in, our biogeographic-representation criterion. The first of these criteria highlights the fact that there may also be biogeographic patterns in the distribution of habitats. Representation of habitats is dealt with more directly in the criterion below, but regardless of whether conservation effort is focused on species or habitats, we must provide protection in all biogeographic regions. The second of these criteria draws attention to another important facet of biogeographic representation, the inclusion of reserves in transition zones between biogeographic regions. Inclusion of reserves in both transition and core areas will help protect genetic diversity, providing a proxy measure for an aspect of biodiversity that is rarely considered separately. Reserves in transition zones are also ideally placed to monitor shifts in distribution of species arising from climate change (Barry et al. 1995).

Reserves in transition zones could also help build resilience of species to shifts in the boundaries of biogeographic regions, such as can be caused by regime shifts. For example, cold temperate fish species in the Southern California Bight have suffered long-term reductions in recruitment due to anomalously warm conditions (Roemmich and McGowan 1995, Love et al. 1998). Recovery following restoration of more normal water temperatures may be slow because intensive exploitation has depleted spawning stocks (Love et al. 1998). By protecting long-lived adults, reserves in this region could have helped sustain spawning stocks through lengthy recruitment lows and thereby fostered faster recovery.

Habitat representation and heterogeneity

Once biogeographic regions have been defined and agreement reached on the need to conserve representative sections of each region, the next decision is where the reserves should be placed within regions. One of the most important criteria is to ensure protection of all the major habitats present (Day and Roff 2000). This requires much less information than if species themselves were used as a basis for reserve selection (Ward et al. 1999). Habitats can be defined in several ways. For example, some are defined primarily on their physical characteristics (e.g., rocky shores are intertidal and have a hard-rock substrate) while others are mainly recognized by their biological attributes (e.g., mangroves are only mangroves because of the dominant role of their trees; see Day and Roff 2000 for more examples).

Representing all habitats is an essential objective for a network of reserves. However, habitat heterogeneity can be used to guide the selection of individual reserve units. If two or more rival areas are being considered

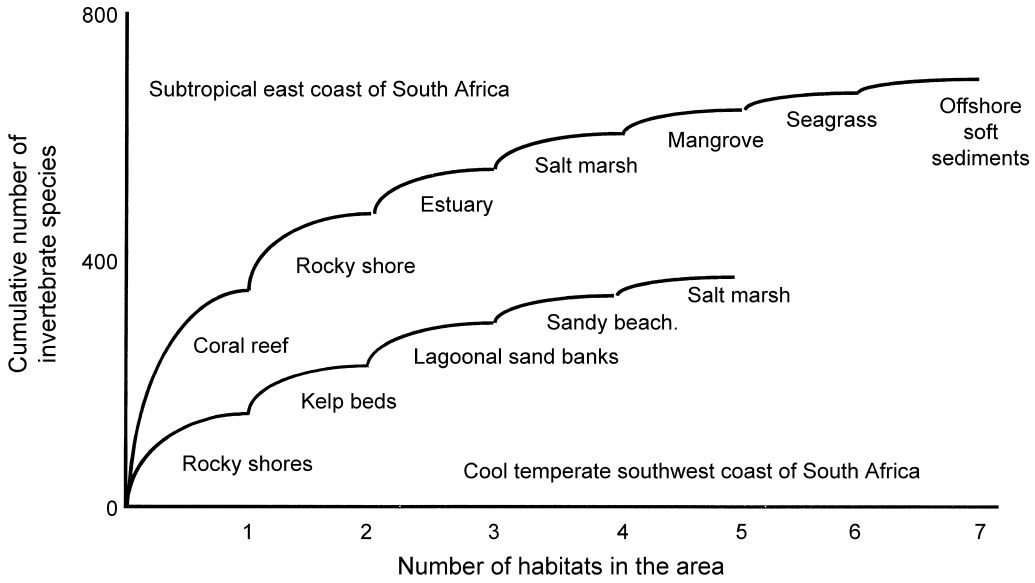

FIG. 1. The relationship between habitat diversity and the number of invertebrate species recorded in two areas (Maputoland, a subtropical area on the east coast of South Africa, and Groenrivier, on the west coast of South Africa). In each area, data were obtained from 10 quadrat samples of 0.5 m^2 for each habitat, and the number of species plotted cumulatively for each of the 10 quadrats. Habitats with the highest diversity were plotted first, followed by habitats with successively lower values. With the addition of each habitat, species were excluded from the count if they had already appeared in the count for previous habitats.

as reserves, one of the prime factors for their evaluation should be habitat heterogeneity (the number of habitats they contain; Hockey and Branch 1997). As the number of habitats within it increases, so does the value of a site for a reserve. This acts as a proxy for maximizing the number of species protected. In many parts of the world we do not have the luxury of taking the time to document, on a sufficiently fine spatial scale, what species are present (let alone their relative abundance). The ideal of comprehensive comparisons among sites based on species richness or diversity is an unrealizable dream. Under these circumstances, habitat heterogeneity becomes the only alternative measure that can be applied.

As an example, Fig. 1 shows the relationship between habitat diversity and species richness for two different localities on the coast of southern Africa. Two things emerge. First, as more habitats are added to a conserved area, species richness progressively increases. The relationship is not linear because all habitats are not equally species rich, and most share some species. Second, different localities differ in their overall species richness, even if they possess a similar range of habitats. Tropical areas are almost invariably more speciose than temperate areas. This means that different biogeographic regions cannot be compared directly: habitat heterogeneity can only validly be compared between sites within regions.

A stretch of coast that combines a large number of habitats will have several advantages as a site for a reserve. First, it will include a greater diversity of species than an area comprising only a single habitat. Second, it has a fighting chance of conserving an array of functioning ecosystems. Third, when interconnections occur between ecosystems or habitats, conserving several in a single area helps protect the flows between systems, rather than relying on inputs from separate protected areas placed at a distance. For example, many species undergo different phases of their life cycles in different habitats, moving between them as they develop (Appeldoorn et al. 1997). Links among mangrove and sea-grass nursery areas and coral reefs are well known (Ogden and Gladfelter 1983, Roberts 1996, Nagelkerken et al. 2000). The Hol Chan Marine Reserve in Belize links all three habitats, although at present only the coral reef in it is fully protected (Carter and Sedberry 1997).

By using habitat heterogeneity rather than species richness as a measure of the desirability of an area, one overcomes the problem that different habitats are intrinsically different in species richness. To exemplify, coral reefs always have a higher diversity of species than sandy beaches, but that alone should not make them any more valuable in terms of conservation priority. Also, there is the nonscientific but important fact that physically heterogeneous areas are those that most people regard as aesthetically appealing. One cautionary note must be added when ranking sites according to habitat heterogeneity. If a small area is divided into many habitats, there is the risk that each will be too small to be viable (a viable habitat is one which supports populations capable of long-term persistence).

When evaluating an area, common sense dictates that tiny, unsustainable habitats should be excluded from consideration. Exactly what reserve size is too small is a difficult question to answer and requires more empirical and theoretical study (see later).

Human threats

The establishment of fully protected marine reserves intrinsically acknowledges the threat posed by consumptive or extractive human use of marine resources and the bycatch and/or habitat damage often associated with these uses. A number of other threats may seriously affect the viability of a marine reserve and preclude it from meeting its intended objectives. For these reasons, consideration of past, present, and foreseeable future influence of human activities on a candidate site is important. Human threats occur on a variety of spatial and temporal scales and it may be possible to mitigate some of them through complementary coastal-management efforts. Other threats may not be mitigatable. To be effectively employed as a criterion for selecting marine reserves, mitigatable and nonmitigatable human threats should be identified and quantified, where possible. In many cases, a site may be exposed to more than one threat. For example, proximity to urban centers may confer increased fishing, visitation pressure, and greater contamination.

Fishing pressure may have both positive and negative implications for the consideration of reserve sites. Some types of fishing pressure might increase the priority of a site as a reserve because their unwanted effects could be lessened or overcome by protection. Indeed, sustaining fisheries is a goal of reserves and there is evidence that reserves can improve yields in adjacent areas (Alcala 1988, Castilla 1999). However, very intense fishing might exclude a site from consideration. Fishing pressure may cause habitat shifts through trophic cascades or actual physical damage (Sala et al. 1998, Watling and Norse 1998). Areas that can potentially recover after protection from intensive fishing should be included, but not those where serious structural damage means this is unlikely.

Natural catastrophes

Every environment exposes organisms to stresses that reduce their capacity to reproduce. In extreme cases these stresses lead to death. The impact of these stresses will depend on their magnitude, duration, and frequency. There are four circumstances in which stresses are likely to exceed the tolerance limits to which organisms are adapted: (1) if the stress is prolonged; (2) if it reaches extremes; (3) if it occurs with great rapidity; or (4) if its occurrence is too infrequent for adaptation to it. All these events are unpredictable, and include infrequent diseases that decimate populations (Miller and Colodey 1983, Lafferty and Kuris 1993), earthquake-induced uplift of rocky shores (Castilla 1988), irregular floods (Branch et al. 1985, 1990), abrupt temperature shifts associated with intermittent upwelling, unusually prolonged low tides, and low oxygen levels induced by harmful algal blooms (Hallegraef 1993, Matthews and Pitcher 1996, Hopner and Oelschläger 1997).

A feature of all these disturbances is that reserves will grant no protection and so areas with frequent episodic catastrophes are least attractive as reserves. It is often possible to identify stretches of coast where catastrophic events are concentrated. For example, eruptions of hydrogen sulfide are regular events on the northern Benguela Current, particularly off Walvis Bay, and lead to periodic mass mortalities of fish (Copenhagen 1953). Further south, there are two areas on the South African coast renowned for periodic red tides. These become so intense they deplete oxygen and even generate hydrogen sulfide, leading to mass mortalities. At one of these sites, Elands Bay, red tides led to three successive ''walkouts'' of rock lobsters in a single year, with over 2000 Mg of rock lobsters becoming stranded on the shore in an attempt to escape low-oxygen waters (Pitcher 1999). At the other site, St. Helena Bay, there have been three mass mortalities over six years, including the death of over 400 Mg of rock lobsters. Ironically, St. Helena Bay is precisely the site selected for a rock-lobster sanctuary.

Quite clearly, areas that are focal points for episodic catastrophes make poor candidates for reserves, since species will have to recolonize from elsewhere following disturbance. The more frequent the disturbance, the less desirable a site (Allison et al. 2003). One way of overcoming the problem of catastrophes is to spread risk through replication of reserves. Data on the frequency and location of episodic catastrophes could be used to help provide rough guidelines for spacing and numbers of reserves required (H. Possingham, S. Andelman, S. Gaines, L. Botsford, A. Hastings, and J. Lubchenco, *unpublished manuscript*).

Size

The question of size of marine reserves can come in two forms. First, if a large total area is available for protection, how does one best divide (or not divide) that into reserves? Alternatively, if a particular location requires protection, how big should a reserve be in order to provide it? Answers can be different in different situations and may depend on the purpose of the reserve.

In an analysis of 89 studies of fully protected marine reserves, Halpern (2003) showed that in virtually every case, the creation of reserves led to increases in abundance, biomass, size, and diversity of organisms. The magnitude of these effects was independent of the size of the reserve (the size range examined was 0.002–846 km^2, with a median of 4.0 km^2). In other words, both small and large reserves produced similar increases in

each of the measures. Thus the aggregated biological benefits of reserves increase directly with the total area protected, regardless of how this is subdivided into reserve units. Based on how much benefit is desired, a total area or proportion of habitat can be specified for protection (National Research Council 2000, Roberts and Hawkins 2000). Because many biological effects of reserves do not appear to be size dependent, decisions about the actual size and distribution of reserves should focus on other issues.

Before discussing these issues, it is important to appreciate the limitations of Halpern's (2003) study. The taxonomic range of species examined in this study was rather limited, and the quality of data presented variable; hence only quite crude aggregate measures of performance were possible. These aggregate measures obscure the range of species-specific responses to reserves and their possible dependence on reserve size. Furthermore, no measures of ecosystem processes were included, only of species present, and such processes may also be sensitive to reserve size.

Export functions.—The large edge-to-area ratios of small reserves make them better at exporting larvae and adults. This is important for meeting both fishery and conservation objectives: export to fishing grounds will help support yields (Alcala 1988, Castilla et al. 1998), while export to other reserves will promote long-term population persistence. Fishery export is best served by subdivision of protected areas across the region of interest. This will provide local benefits to fisheries, through juvenile and adult spillover, and more regional benefits, through greater larval export. For this reason, many small reserves in a network would be preferred over fewer large ones.

Viability.—Small reserves, however, may not support populations that are large enough to persist, especially for mobile species that often cross reserve boundaries (increasing mobility diminishes the effective size of a protected area; Kramer and Chapman 1999). If populations cannot sustain themselves, the reserve will not serve either fishery, conservation, or other objectives dependent on those species. Halpern's (2003) conclusion that even small reserves increase abundance and diversity of organisms probably stems from the protection of species that are recruited from elsewhere, i.e., reserve populations maintained from other source populations. This is an important point: very small reserves will function only to the degree that essential linkages to other habitats are maintained. Such linkages will influence the size of habitat fragments in reserves that will be viable. Where a habitat is abundant in a region, small fragments are more likely to be viable than if the habitat is rare, since linkage to other sources of recruits will be greater for abundant habitats. Hence, viability must be viewed in the context of habitat extent and distribution. Larger reserves will probably be needed to protect rare and fragmented habitats as compared to extensive and well-connected habitats. If a particular habitat patch is the only representative in a local area of that habitat, it will be at higher risk than a patch with several other similar habitat patches in the vicinity. Viability of habitats in reserves will also depend on the protection status of other similar habitats nearby. Where many habitat patches are protected, their viability in reserves is likely to be greater than where no other examples of that habitat are protected (Roberts 2000).

There is no simple cutoff point in size where a habitat patch slips from being viable to inviable. The critical area will be different for each species the habitat supports. Ideally, it will be possible to protect habitat patches of sufficient size that populations of all species present will be viable. However, under some circumstances, reserves may be designed with particular species in mind, for example species listed as endangered. The patch sizes of habitat needed for such species might be determined using population viability analysis (PVA), which has had some success in influencing terrestrial reserve design. However, there are few PVAs for marine species and the argument for a single-species approach to conservation planning may be even weaker in the sea compared to on land. Where threatened species are a focus of conservation action, other steps may be necessary to assure populations are viable. For example, if a species is sensitive to Allee effects and has fallen below critical population densities needed for successful reproduction, it may be necessary to artificially increase densities in reserves (National Research Council 2000). For example, this may be the only way to restart reproduction by species like the critically endangered white abalone (*Haliotis sorenseni*) in California, whose global population is estimated at no more than a few hundred widely scattered individuals (Tegner et al. 1996).

Finally, populations of some species will only be viable if networks of habitat patches are protected that include vulnerable life stages (for example, spawning aggregations; Johannes 1998). A single reserve cannot encompass the necessary range of areas necessary to ensure persistence (see *Selection critieria*: *Vulnerable life stages*).

Disturbance.—Small reserves are more vulnerable to periodic disturbances, such as extreme low tides or algal blooms, that could wipe out a reserve population in a single event. Larger reserves can help mitigate this vulnerability, but they also risk ''putting all your eggs into one basket.'' A catastrophic event could drive entire populations to extinction in a single large reserve, whereas creating smaller reserves within a large network might avoid such a fate. This points out one of the important tradeoffs between reserve size and reserve number. For example, Washington State (USA) has three reserves for razor clams (*Siliqua patula*). Clams in one of them were recently wiped out due to

a shift in the course of a river while those in the remaining two were unaffected (D. Simons, *personal communication*). If all the area had been placed in one reserve, none of the clam population might remain protected.

Management.—Logistical concerns also weigh heavily in decisions about how big to make a reserve. Though many small reserves spread risk, they are often much harder to enforce than a few large ones, and a vast network of small reserves may prove too complex for compliance. Larger and fewer reserves offer easier enforcement because they allow concentration of monitoring effort as well as making it easier for people to recognize and adhere to reserve boundaries. However, larger reserves may be more difficult for people to accept, especially in intensively used areas. These concerns are important since the degree to which reserves support higher abundance, biomass, and diversity of organisms is directly linked to the degree of compliance with closure to fishing (Roberts 2000).

Given the above considerations, we need not become fixated on a particular reserve size. A network of many moderately sized reserves preserves functions over a relatively large area and appears to be a good compromise. However, some variation in reserve size is important. In the few very large reserves some areas of almost pristine ecosystem may be retained, while small- and medium-sized reserves suit many species, spread out risk, and help capture ecosystem variability.

Halpern's (2003) analysis gives us cause for optimism that small reserves can be beneficial. However, the nature of the data he reviewed did not allow him to resolve whether larger reserves would be necessary to benefit larger bodied or more mobile species, but this is likely to be so. Clearly, a network of tiny reserves will be utterly inadequate to protect biodiversity or the processes underpinning it. It is critical to view reserve size in the context of the total area covered. The most important point is that the greater the combined area covered by reserves, the greater their absolute benefits. Present evidence suggests that protecting 20% or more of each habitat present will be necessary to support fishery production and safeguard biodiversity over the long term (National Research Council 2000, Roberts and Hawkins 2000).

Connectivity

Several forms of connectivity are important to marine reserve function: (1) the exchange of offspring, (2) the movement of juveniles and adults, and (3) the transfer of materials, such as organic carbon. Here we deal only with the exchange of offspring. Adult and juvenile movement is discussed elsewhere in relation to habitat heterogeneity and the protection of vulnerable life stages. Movement of materials is covered in *Selection criteria*: *Ecosystem linkages.*

Exchange of offspring between places is critical to the functioning of reserves, especially as conditions outside reserves deteriorate. It can affect both sustainability of populations inside a reserve and the degree to which a reserve can serve as a source of recruitment to fishing grounds. In siting reserves two questions must be asked: (1) Is there sufficient connectivity to allow exchange and replenishment within the reserve? and (2) Will populations in a reserve connect with others in unprotected areas or in other reserves? The answers to both questions depend on dispersal distances for the organisms protected (most marine species have a pelagic larval-dispersal phase), reserve size, and local oceanography. Populations in isolated reserves will only be self sustaining where there is significant local retention of offspring. By contrast, for fishery enhancement to occur there must be substantial export of offspring. Perhaps the perfect reserve could be viewed as one where there is sufficient local retention to sustain populations inside the reserve, but the majority of offspring are exported and will replenish fishing grounds. Given that most marine species are highly fecund, such a situation may not be unusual. It would take only a small fraction of the fecundity to provide replenishment, and the survival of this fraction might be quite high relative to the fate of larvae dispersed further afield. For example, 90% of the recruits in a reserve could result from retention, but these recruits could represent only 1% of local production. The other 99% of local production could be exported to fished areas and to other reserves if these are located within dispersal distances. Because species' dispersal characteristics vary widely, the ideal distribution and sizing of reserves for one species may be very different from that for another (Roberts 1998, Shanks and Grantham 2001, Grantham et al. 2003).

At a single-species level, site selection may substantially affect the degree of self-sustainability and connection to other areas. Past work suggests that areas may differ substantially in the degree to which they depend on local production for recruitment. On the Caribbean island of St. Croix, for example, Swearer et al. (1999) found that the leeward end of the island had the highest recruitment of bluehead wrasse (*Thalassoma bifasciatum*), and that recruitment pulses were retention events. Windward reefs received less recruitment, and most larvae came from elsewhere. Thus differences appear even in areas in close proximity, with populations deriving from a mix of local and more distant sources of recruits. In addition, one habitat may affect another's recruitment by simply intercepting potential settlers, creating downcurrent ''shadows'' of low recruitment or filtering some potential settlers out of the larval pool (Jones 1997). Regardless of the purpose envisioned for a reserve, it is essential that network design consider dispersal distances (Ruckelshaus and Hays 1998) and the protection of larval habitat

(Carr and Reed 1993). While larvae are not fished directly, they could be affected by pollution or habitat destruction (Allison et al. 1998).

If recruitment is influenced by larval retention, then reserve design will be affected in many ways. Where local retention of offspring is low, sustainability of reserve populations will depend on replenishment from elsewhere, either from other reserves or from any reproductive populations in unprotected areas (Gerber et al. 2003). If the reserve is expected to export larvae to replenish fished areas, then the location should preferably be in nonretention areas. However, this is a double-edged sword: if all production is exported, there may be no source of recruits for the reserve itself (Carr and Reed 1993). It may also be less resilient in the event of a local catastrophe that lowers biodiversity because of the lack of outside sources for replenishment. This will become a critical issue if reserves are to be used as fishery-management tools (e.g., Bohnsack 1996, Lauck et al. 1998). If management schemes become overly dependent on reserves, there may be a corresponding relaxation of traditional management methods. This might lead to heavy exploitation of fished areas, which would reduce potential sources of recruits for the reserves themselves, unless reserves are closely networked (Carr and Reed 1993, Allison et al. 1998).

For species highly vulnerable to overexploitation, reproductive populations may become depleted in fished areas, and so sources of recruits are likely to be from other reserves. For species that are not exploited or are more resilient to exploitation, there will probably still be significant reproduction in unprotected areas. The rate and extent of recovery of communities inside reserves may depend on the intensity of fishing outside the reserve. Where source populations are intensively exploited, reserve populations may only recover slowly, or may fail to reach the potential carrying capacity of the habitat due to recruitment limitation (Roberts 2000). For example, in Jamaica, fully protected marine reserves have failed to show any buildup of larger snapper and grouper species (M. Watson, *personal communication*). Local source populations have been so overexploited that there are no fish left to provide recruitment to reserves. By contrast, in the British Virgin Islands, which have been less heavily exploited, recruitment of snappers and groupers is several orders of magnitude higher and populations in reserves established there are expected to build up quickly. Man et al. (1995) provide theoretical support for the suggestion that the worse the conditions in unprotected areas, the more reserves are required.

Vulnerable habitats

Habitats especially vulnerable to disturbance may deserve particular consideration for inclusion in reserve networks, provided they can be effectively protected. These include habitats with low ecological resilience (Folke et al. 1996), such as coral reefs and salt marshes, and regionally rare or threatened habitats.

Nonresilient habitats are often characterized and maintained by some type of biological matrix or structure rather than physical structures or processes alone. The ecological integrity and functioning of mangrove forests, sea grass beds, salt marshes, and coral reefs and their associated lagoons all depend on a biologically generated matrix. Perturbation or loss of that living matrix destroys the integrity and functioning of the entire ecological community. Recovery of the biological matrix and habitat may require years following major disturbance (Rogers 1990, Bythell et al. 1993, Hughes 1994, McCoy et al. 1996). Further, fragmentation of the matrix by smaller scale disturbances can erode habitat functioning and reduce resilience (Creed and Filho 1999). Many of these nonresilient habitats occur in shallow coastal areas where human development is also concentrated, adding further need for their conservation.

Recovery of sea grasses and some macroalgal matrices may depend on the damage to rhizomes or holdfasts. Experimentally cleared and trampled plots of seaweeds and mussels in the rocky intertidal recovered to a mere 30% and 25% of pretreatment and control values in 10 yr (Richards 1994). In some cases, the original biological matrix may be replaced by species which do not provide the same type of matrix, and this may persist for years. For example, recovery of brown mussel (*Perna perna*) beds may take more than eight years, in part because algae replace the mussels following disturbance and mussel beds are the preferred settlement substrate for recruits of *P. perna* (Dye et al. 1997). Loss of the biological matrix may also influence the success and spread of invasive species. In southern California bays, an invasive mussel (*Musculista senhousia*) had lower growth and survival in beds of native eelgrass (*Zostera marina*) than in disturbed habitat with no eelgrass (Reusch and Williams 1999). Beds of the invasive mussel also had negative effects on rhizome growth and vegetative propagation of native eelgrass.

Habitats that are regionally rare or threatened may need higher consideration in marine-reserve networks. For example, coastal wetlands of southern California have been reduced to ~10% of their former coverage over the last 300 yr (Zedler 1984). Additional loss, isolation, and fragmentation of this habitat may further compromise viability and ecological functioning on a regional basis. Rocky shores are ecologically rich, yet in many regions comprise a small fraction of the coasts. For such habitats, a larger proportion may need to be included in a reserve network to ensure viability. Rare habitats are by their nature vulnerable to change and elimination and may well be irreplaceable within a region.

Vulnerable life stages

Identifying life-stage transitions that are critical to a species' population dynamics can be useful in choos-

ing among sites for inclusion in a reserve network. Where vulnerable life stages are known, the habitats or processes supporting them should be protected. For example, many organisms have life histories that include aggregation spawning or breeding, migration bottlenecks, or other habitat-specific ontogenetic transitions. Habitat characteristics can have an effect on survival probabilities within a life stage, and they can affect critical transition probabilities between life stages (M. Ruckelshaus and J. Dugan, *unpublished manuscript*).

A common method of identifying vulnerable life stages is to use a matrix population model (Caswell 1989) that can show how a change in each demographic parameter affects population growth rate. M. Ruckelshaus and J. Dugan (*unpublished manuscript*) found that for 17 species they reviewed, recruiting juveniles and individuals up to smaller reproductive sizes were most often critical to population dynamics. However, for three species, a seaweed and two polychaetes, vulnerable life stages varied among locations and years.

If potential reserve sites contain habitat that supports vulnerable life stages for one or more species, those sites may be given higher priority than others. Understanding which life stages are most critical to population dynamics can help avoid misdirected site selection. For example, the most effective way to enhance population growth of loggerhead sea turtles (*Caretta caretta*) is to enhance juvenile survivorship (Crouse et al. 1987). Most efforts at sea-turtle conservation have focused on protecting eggs on nesting beaches. Crouse et al.'s analysis suggested this would have little effect on population size. Instead of a reserve including nesting beaches, one protecting sea-grass habitats, where juvenile turtle bycatch in shrimp fisheries is high, may be more productive. However, on the east coast of South Africa, where there is no equivalent threat from shrimp fishing, protection of nesting sites has led to substantial population recovery (Hughes 1989).

Use of matrix population models is limited by heavy data requirements, the difficulty of keeping track of marked individuals, and the assumption that populations are closed, with local recruitment dependent on local production (Caswell 1989). Due to larval dispersal, many marine species appear to have much more open dynamics. Without knowing what fraction of larval production from one area contributes to adult abundance, the relative importance of different life-stage transitions cannot be predicted.

For the vast majority of species being considered for inclusion in a reserve network, the information necessary to perform a formal demographic analysis will not be available. What guidance can we offer in these cases? For one, it is useful to note the number of habitats species occur in throughout their life cycle. Some species will spend their entire life within the habitats contained within a single reserve, and others may use multiple habitats throughout their life cycle, including habitats outside of a reserve network. For example, a number of fish and crustacean species use estuaries or nearshore sea-grass habitats early in their life history and then migrate into deeper habitats offshore for feeding and spawning (Wallace et al. 1984). Ideally, all important habitats should be networked in reserves.

Some species are particularly susceptible to mortality or stress when they are concentrated in space, such as during migration bottlenecks or spawning aggregations. A classic example is the concentration of squid (*Loligo vulgaris reynaudii*) to mate and lay eggs in well-defined grounds where they become easy targets for fishing (Sauer et al. 1992). Similarly, shorebirds undertaking long-distance migrations aggregate in lagoons and estuaries to feed (Hockey et al. 1992) and could suffer if these habitats become degraded. When possible, reserve siting should include consideration of these vulnerable stages and the habitats in which they occur (Warner et al. 2000). It may be important to include several, linked life stages in reserves, otherwise protection of spawning areas could redirect fishing effort into juvenile nursery grounds, increasing mortality rather than reducing it (Horwood et al. 1998).

Species or populations of special concern

Some species or populations have characteristics that make them of particular interest for inclusion in reserves. Species that are unique to a particular region (endemics) are often afforded higher conservation priority than species that are more widespread (International Council for Bird Preservation [ICBP] 1992). Narrowly distributed species are considered to have a higher risk of extinction than widespread species because a localized impact could affect their entire range. However, the term endemism is often loosely applied, and this can lead to value judgements about which species to include. For example, a species may be found only in Canadian waters and so is endemic to the country, but might be very widespread within the country's waters. Alternatively, a species might be restricted to a few fjords along the northwest Canadian coast but might be afforded equal value in conservation decisions. Endemism is a spatially ambiguous concept and tends to be used loosely at arbitrarily defined spatial scales.

A second problem with using endemism, in the sense of species that are restricted to a particular geographic or political unit, is that this definition may lead to bias in evaluating the conservation priority of a site. For example, places close to the edge of a country are likely to contain fewer endemics than areas close to the center, since species' range boundaries at marginal sites are more likely to overlap adjoining countries. Thus centrally located sites might be assigned artificially inflated conservation values.

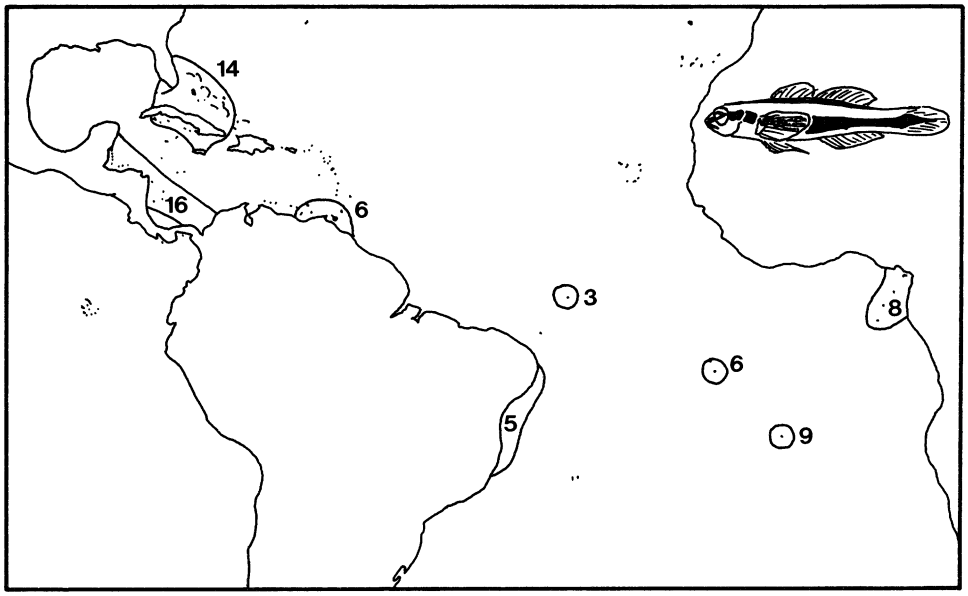

FIG. 2. Endemism hotspots for coral-reef fishes in the tropical Atlantic based on an analysis of the global geographic ranges of 363 species of fish. The locations marked indicate sites where there were three or more species of restricted-range fishes present, defined as species with range sizes of $<800\,000$ km^2. Reproduced from Roberts et al. (2002), with permission.

To overcome these problems and provide more objectivity, endemism is now more usually substituted by the concept of restricted range. Conservation value is assigned to species based on the size of their global geographic range. ICBP (1992) has used a breeding range of 50 000 km^2 or less as an arbitrary cutoff point to define restricted-range species on land. In the sea, Hawkins et al. (2000) have used an arbitrary cut off point of 800 000 km^2, reflecting the generally larger range sizes of marine species. In applying this criterion, the value of sites can be determined according to the number of restricted-range species present. This kind of assessment can be made at a variety of scales. Fig. 2 shows, for example, endemism hotspots for coral-reef fish in the tropical Atlantic.

As an alternative to using an arbitrary cutoff point for what constitutes a restricted range, it is possible to measure range rarity, which is the reciprocal of the range size of a species. If the value of range rarity is calculated for each of the species present in the area being considered for reserves, then different sites can be compared by using the sum of the range-rarity values for all of the species present at any given site (see Roberts et al. [2002] for an example).

To implement this criterion, sites would be selected based on either the number of restricted-range species or the summed range-rarity values for the species present. The site that had the highest value according to one or other index would be selected first and subsequent sites could be added through an analysis of complementarity that would ensure inclusion of unrepresented species.

Relict species have also been identified as being of special concern. Relicts are species that have persisted in particular regions following contraction or fragmentation of previously more extensive distributions over evolutionary timescales. The presence of such species, especially if there were many of them, would add value to sites being considered for reserves, due to their scientific interest. For example, the two known coelacanth species (*Latimeria chalumnae* and *L. menadoensis*) in the Comores and Indonesia appear to be geographically very restricted, their populations have highly specific habitats from which there is little movement, and they are threatened by artisanal fisheries in which they are bycatch (Erdmann 1999, Hissmann et al. 2000). They represent ideal candidates for protection in fully protected marine reserves.

Another category of species of special concern includes those that are rare wherever they occur, even if geographically widespread. Rarity in itself does not necessarily mean that population viability is low (Gaston 1994), but it can render a species more vulnerable to human impacts than if it were more common. In many cases, rarity may be a direct result of exploitation. When this is the case, fully protected reserves can directly protect rare species. For example, among the giant tropical groupers, the jewfish (*Epinephelus itajara*) has now disappeared from most of its former range in the Caribbean, while an Indo-Pacific congeneric, *Epinephelus tukula*, is now extremely rare (Morris et al. 2000).

Targeting globally rare species deliberately excludes species that are simply rare because they are at the

edges of their ranges or in otherwise marginal habitat. Conservation concern for the latter species is much lower. While many countries do attach conservation importance to locally rare species, populations of species at the edges of their ranges may be very hard to sustain. Their numbers tend to fluctuate widely (Lesica and Allendorf 1995) and reserves may be unable to support viable populations over the long term. However, the term ''globally rare'' can be applied to species that have pockets of higher abundance in an otherwise sparse distribution. Southern Florida, for example, is a last stronghold for the jewfish as its extensive areas of mangrove and sea grass provide excellent juvenile habitat (Bullock et al. 1992). This locality has probably always been a core habitat for jewfish, even when they existed throughout much of the Caribbean.

Identifying species that are globally rare requires information on their abundance throughout the whole of their range. This may extend far beyond the boundaries of the region being considered for reserve establishment. Such information may also be hard to come by. Our knowledge of marine species, especially small-bodied organisms, is generally poor and so many species that could qualify will be missed. This approach is most applicable to larger and well-known taxa.

It is also possible to consider the genetic diversity of populations in selecting reserve sites (Palumbi 2003). All else being equal, sites containing populations characterized by greater genetic diversity should be given greater priority. In theory, these populations have a greater evolutionary potential, or ability to adapt to changing environmental conditions (Lesica and Allendorf 1995). However, the reserve-selection process developed in this paper is directed toward achieving multiple objectives and we would not recommend that the genetic diversity of populations of a single species should dictate, or even heavily influence, site selection. Knowledge of genetic structure is always likely to be limited to a small number of species, whereas selecting reserve sites that serve entire communities of species should usually be the objective.

Exploitable species

Halpern's (2003) review of reserve effects provides powerful evidence of the capacity of reserves to enhance stocks of exploited species and simultaneously protect biodiversity. However, for such reserves to fulfill fishery-management objectives they must either actually protect populations of exploitable species or be capable of protecting them. The latter distinction is important since populations of exploitable species have often been severely depleted and reserves are being considered as a means of rebuilding stocks. One possible guide to whether an area might support a species is whether it did so in the past. For example, in the Caribbean, several species of grouper in the genus *Mycteroperca* were formerly common on reefs but have been virtually extirpated as a result of intensive fishing (Roberts and Hawkins 1999). Most reefs are presumably still capable of supporting these species if sections were to be closed to fishing. The choice of reserves in San Juan County, Washington State, USA, was guided by fishers identifying places that were excellent fishing sites in the past (Murray 1998). However, one problem with using past abundance as a guide to the possibility for recovery is that if populations have been eliminated over a large area, lack of recruitment may limit recovery (Tegner et al. 1996).

The potential for exploited species to recover may also be limited where depletion or other human impacts, such as development or pollution, have disrupted fish behavior or movements. For example, in the Caribbean, Nassau groupers (*Epinephelus striatus*) once spawned in aggregations that numbered tens of thousands of fish (Sadovy 1993). However, throughout much of the eastern Caribbean those aggregations have been fished to the point of disappearance and the species may fail to recover because remaining individuals cannot effectively reproduce outside such aggregations.

The potential for recovery inside reserves may also be limited by modification of habitats. For example, in the North Sea, habitats on the Dogger Bank were dramatically changed by the advent of trawling in the mid-nineteenth century (Alward 1932). Trawling transformed the habitat from something suitable for many species of gadoid fish, to a habitat more suitable for flatfish such as plaice.

Despite the foregoing caveats, the overriding message from empirical (Halpern 2003) and theoretical work (Gerber et al. 2003) is that marine reserves can and do lead to the recovery of exploited species.

Ecosystem linkages

In many parts of the world, apparently disjunct but juxtaposed marine and terrestrial systems have been shown to be interdependent (Newell 1984, Suchanek et al. 1985, Mann 1988, Duggins et al. 1989, Mann and Lazier 1991, Bustamante et al. 1995, Polis and Hurd 1996, Garman and Macko 1998). Many types of linkage can be recognized, but we concentrate here on those that have a trophic basis because ecosystem functioning is often defined in terms of the performance of a food web. We only consider linkages that are relevant to marine-reserve selection. Many linkages are mediated by species or functional groups (e.g., mangrove litter supplies sea-grass communities, or subtidal macroalgae subsidizes intertidal or terrestrial communities). Consequently, linkages are defined here as the flow, or impediment, of materials from one system to another that allows, modifies, or modulates the functioning of a given marine and coastal area.

Perhaps the best documented marine and coastal linkage is the role of macrophyte-derived matter as a

connection between the food webs of subtidal, intertidal, and estuarine ecosystems (Duggins et al. 1989, Bustamante et al. 1995, Bustamante and Branch 1996, Soares et al. 1996, 1997, Rodriguez 1999). Such linkages, termed ''trophic subsidies,'' can increase the secondary and tertiary production of the receiving ecosystem (Duggins et al. 1989).

The operative use of this criterion for the selection of marine reserves is not straightforward, but its implications are highly relevant. For example, sessile benthic fauna are often trophically dependent on external inputs and production processes. Hence, inputs of organic matter via detrital pathways must be considered when selecting reserves that will protect benthic communities. This is especially important as the benthic biomass of most reefs, beaches, lagoons, or estuarine ecosystems is often dominated by benthic filter feeders or suspension and deposit feeders. Many studies have demonstrated that the abundance, growth rates, and standing stock of suspension feeders are mediated by trophic subsidies from adjacent ecosystems or communities (e.g., Albert and Valiela 1995, Bustamante et al. 1995, Slim et al. 1996, Duggins and Eckman 1997, Irlandi and Crawford 1997, Soares et al. 1997). Consequently, conservation of habitats or ecosystems that contain such important groups of basal species (sensu Menge 1992) will depend on the selection of sites within a network that include the donor ends of all identified linkages. For example, network sites containing kelp forests will need to complement intertidal rocky-shore reserves that are dependent on them, and mangrove forests supplementing sea-grass communities should be included in the reserve design.

Despite their obvious importance, ecosystem linkages have not been fully explored or used in the decision-making process of designing and setting up marine reserves. Again, linkages cannot be used in isolation, but their use as a criterion can alter or modify the decision-making process when choices need to be made between rival sites being considered for protection. They are also an important consideration for the long-term success of a given marine reserve. A coastal reserve of small islands, designed for the conservation of particular faunal communities that include invertebrates and seabirds, may not succeed if the nearshore marine communities are not included (Polis and Hurd 1996, Polis and Strong 1996).

Ecological services for humans

Ecosystem services are benefits provided to humanity and other life on Earth as a result of the functioning of ecological systems (Daily 1997). Virtually all ecological systems provide services. The provision of goods, such as fish supplies, is an obvious and vitally important service. Intact ecological systems are essential to provide the services that humans use.

Many services operate over local scales. For example, mangroves and coral reefs protect coastlines from wave action. Wetland plants in reed beds, salt marshes and mangroves trap and filter sediments. Filter feeders, such as oysters, cleanse water in bays. Biological structures, for example mangrove roots or seagrass beds, create critical habitats for spawning, recruitment, or growth of biota. Healthy ecosystems also provide desirable places for recreation, inspiration, education, and the creation of new knowledge. Some services operate over regional scales, for example detoxification and sequestration of pollutants, generation and maintenance of biodiversity, decomposition of dead biological material and cycling of nutrients. Yet other services operate over global scales, for example the partial regulation of climate and biogeochemical cycling.

Only recently have ecosystem services been recognized as important benefits (Daily 1997). Historically, humans have primarily valued the goods provided by ecological systems, while services have been taken for granted. Because services are largely outside economic systems, changes in quantity are not always obvious, unlike goods which increase in value when scarce (Perman et al. 1996). Together goods and services provide the life support systems for all life on Earth. Ecosystem services are a by-product of functioning ecological systems. If these systems are modified, the services they provide may change.

The study of ecosystem services is in its infancy. Methods to quantify them are under development and the scales over which services are produced are being investigated. Study of the effects of alterations in biodiversity on functioning of ecological systems is another active area of research. Despite the lack of specific knowledge about many critical services, the fact that most are irreplaceable and subject to serious disruption should signal the importance of preserving them.

Application of the Criteria

The criteria described in this paper can be applied in many different ways to the problem of selecting reserves and designing networks. Roberts et al. (2003) have developed a method of applying the full set of criteria in a process aimed at evaluating candidate reserves in the context of their contribution to larger scale networks. They argue that the performance of individual reserves will be enhanced by networking, and that networks are essential to maintain the large-scale ecological processes that underpin ecosystem functioning in the sea. Airamé et al. (2003) show how our criteria can be integrated with social criteria to choose locations for fully protected zones within a large multiple-use protected area—the Channel Islands National Marine Sanctuary in California. Possingham et al. (H. Possingham, S. Andelman, S. Gaines, L. Botsford, A. Has-

tings, and J. Lubchenco, *unpublished manuscript*) take an alternate tack, developing the criteria into a series of rules of thumb to simplify reserve selection. While all these schemes place biological assessment ahead of socioeconomic concerns, they all recognize that socioeconomic considerations will dominate the final stages of site selection. However, use of the criteria can help facilitate decisions by revealing whether candidate sites possess biological attributes that will enable them to meet their objectives.

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